Postembryonic development of appendicular and axial skeletons in *Labeo parvus* (Cyprinidae)

by

Djiman LEDEROUN* (1), Elie MONTCHOWUI (2), Philippe LALÈYÈ (1),
Pascal PONCIN (3) & Pierre VANDEWALLE (4)

Abstract. – The axial and appendicular skeletons in *Labeo parvus* (Cyprinidae) were investigated from hatching to 29 days post-hatch (dph) in cleared and stained specimens. The cartilaginous axial caudal skeleton of *L. parvus* develops like in other cyprinids. The first cartilaginous elements, namely hypurals I and II, appeared 6 dph before notochord flexion. Ossification of the complex begins with that of caudal rays on day 10, next the vertebral bodies, and then all the hypurals on day 14. Dorsal fin development is quite comparable to that of the anal fin. Cartilaginous structures (proximal and distal pterygiophores) appear on day 14 in both fins. Ossification of both fins starts with the rays on day 14, then with the anterior pterygiophores on day 19. Examination of the axial skeleton shows that cartilaginous structures, namely basidorsals and basiventrals, arise on day 14 while ossification begins with the anterior vertebral structures on day 10.

Received: 7 Jun. 2016
Accepted: 7 Dec. 2016
Editor: O. Otero

Résumé. – Développement postembryonnaire du squelette appendiculaire et axial de *Labeo parvus* (Cyprinidae).

Le développement postembryonnaire du squelette axial et appendiculaire de *Labeo parvus* (Cyprinidae) a été étudié, de l'éclosion à 29 jours (j) post-éclosion, sur des larves colorées au bleu alcian et à l'alizarine Red S. Le squelette caudal axial cartilagineux de *L. parvus* se développe comme celui d'un cyprinidé. Les premiers éléments cartilagineux, les hypuraux I et II, apparaissent à 6 j avant la flexion de la corde. L'ossification du complexe débute par celle des rayons de la nageoire caudale à 10 j, ensuite les corps vertébraux et enfin les hypuraux à 14 j. Le développement de la nageoire dorsale est assez comparable à celui de la nageoire anale. Les structures cartilagineuses (ptérygiophores proximal et distal) des deux nageoires apparaissent à 14 j et leur ossification débute par les rayons à 14 j puis les ptérygiophores antérieurs à 19 j. L'examen du squelette axial montre que les structures cartilagineuses, les basiventraux et les basidorsaux, apparaissent à 14 j alors que l'ossification débute à 10 j par celle des corps vertébraux antérieurs.

Key words
Cyprinidae
Labeo parvus
Vertebral column
Unpaired fins
Postembryonic development

Fish is the main source of dietary protein in many countries in West Africa where meat provisions are insufficient or too expensive. It also plays a significant role in the national economy by contributing to reduce unemployment and to meet the protein needs of the people (FAO, 2008). In many West African countries, fish farming has become a requirement for increasing domestic output and reducing currency outflows in the process of importing frozen fish. So far, fish farming in Benin has focused on two main species only: *Oreochromis niloticus* (Linnaeus, 1758) (Cichlidae), introduced within the framework of the "Fish Farming Development" project in the 80's, and *Clarias gariepinus* (Burchell, 1822) (Clariidae), which is a native species. However, other teleost species deserve being introduced and fish-farmed, due to their economic importance as reflected in their increasing use by local populations. This is the case of *Labeo parvus* Boulenger, 1902 (Cyprinidae). This species, with a wide geographic distribution (Lévêque, 2003) is overexploited in the Ouémé basin in Benin (Montchowui *et al.*, 2007; Lederoun *et al.*, 2012). These last 10 years, investigations have been undertaken for its introduction in aquaculture (Montchowui *et al.*, 2007, 2011a, b, 2012a, b, c; Montchowui, 2009; Lederoun *et al.*, 2012).

Information on the development of the skeleton to identify potential abnormalities in the development process of species in captivity is important (Fraser *et al.*, 2004; Kacem *et al.*, 2004; Verhaegen *et al.*, 2007). In this context, Lederoun *et al.* (2012) have established the chronological development of the head skeleton of *L. parvus* from hatching to 29 days post-hatching (dph). However, no study has been conducted so far on the development of the post-cranial skeleton (fins and vertebral column), which, nevertheless, plays

(1) Laboratory of Hydrobiology and Aquaculture, Faculty of Agricultural Sciences, University of Abomey-Calavi, 01 BP: 526 Cotonou, Benin. [laleyeph@yahoo.fr]
(2) Aquaculture School of the Vallée, National University of Agriculture, Porto-Novo, BP 43 Kétou, Benin. [e.montchowui@yahoo.fr]
(3) Behavioural Biology Unit and Laboratory of Fish Demography and Hydroecology, University of Liège, 22 Quai Van Beneden, B-4020 Liège, Belgium. [p.poncin@ulg.ac.be]
(4) Laboratory of Functional and Evolutionary Morphology, University of Liège, Chemistry Institute B6, Sart Tilman, B-4000 Liège, Belgium. [p.vandewalle@ulg.ac.be]
* Corresponding author [ldjiman@yahoo.fr]

an important role in a number of ways. For example, apart from systematic considerations (Monod, 1968; Patterson, 1968; Arratia, 1991; Arratia and Schultze, 1992; Grünbaum *et al*., 2003), morphological studies of the caudal skeleton are relevant in defining the relationship between structure and function, and in establishing how these relationships change during ontogeny (Osse and van den Boogaart, 1995; Grünbaum *et al*., 2003). This paper deals with the chronology of the axial and appendicular skeletons development of *L. parvus*, from the end of hatching up to 29 dph.

MATERIALS AND METHODS

The specimens used in this study are those used by Lederoun *et al*. (2012) while studying the postembryonic development of the cephalic skeleton of *Labeo parvus* in relation to external morphological changes in this species. Larvae and juveniles were obtained from a single artificial reproduction conducted in October 2007 at the fish farming station of the Laboratory of Hydrobiology and Aquaculture (LHA), University of Abomey-Calavi, Benin (Montchowui *et al*., 2011a). The larvae were fed *ad libitum* the first seven days with zooplankton (mainly rotifers and copepods nauplii) produced in the LHA fishponds, and then with *Artemia* nauplii during the following seven days. They were weaned starting from day 15, during four days, with Nippai microgranules. They were fed six times daily (8 am to 18 pm at 2-hour intervals). Average water temperature, pH, dissolved oxygen and nitrites during breeding were 26.8 ± 0.9°C, 7.0 ± 0.3, 6.7 ± 0.3 and 0.04 mg/l ± 0.01, respectively. Thirty specimens were randomly samples. Sampling intervals were as follows: end of hatching, 4 h, 8 h, 12 h, 18 h, 24 h, 36 h, 2 days, 3 days, 4 days, 5 days, 6 days, 8 days, 10 days, 14 days, 19 days, 24 days and 29 days. The fish were fixed in 10% formalin and transferred 4 days later to a 50% ethyl alcohol solution for colouring the vertebral column and the unpaired fins. After being trypsin-cleared, larvae and fry were stained with Alcian blue and Alizarin Red S to highlight cartilage and bone structures, respectively (Taylor and van Dyke, 1985). For each sampled time, these stains were made on separate specimens (Vandewalle *et al*., 1998). After staining, the fish were examined using a binocular microscope Wild M10 and photographed.

RESULTS

Caudal fin development

Two caudal fin developmental stages, 14 and 9 dph are illustrated (Fig. 1), in order to better recognize the skeleton structures during larval development of *L. parvus* (Fig. 2).

Cartilaginous skeleton

Hatching to 5 dph

The caudal end of the notochord is not curved up and carries no cartilaginous element.

6 dph (Fig. 2A)

The caudal end shows two cartilaginous elements: hypurals I and II.

8 dph (Fig. 2B)

The notochord is slightly curved upwards. Hypurals III, IV and V get added to the first two hypurals. The parhypural and the haemal spine 2 are visible.

10 dph (Fig. 2C1)

The notochord is significantly curved upwards.

14 dph (Fig. 2D1)

The notochord definitely takes on the shape of the axial caudal skeleton. The hypural VI, haemal spine 3, uroneural; epural, neural spines 2, 3, 4 and haemal spine 4 appear.

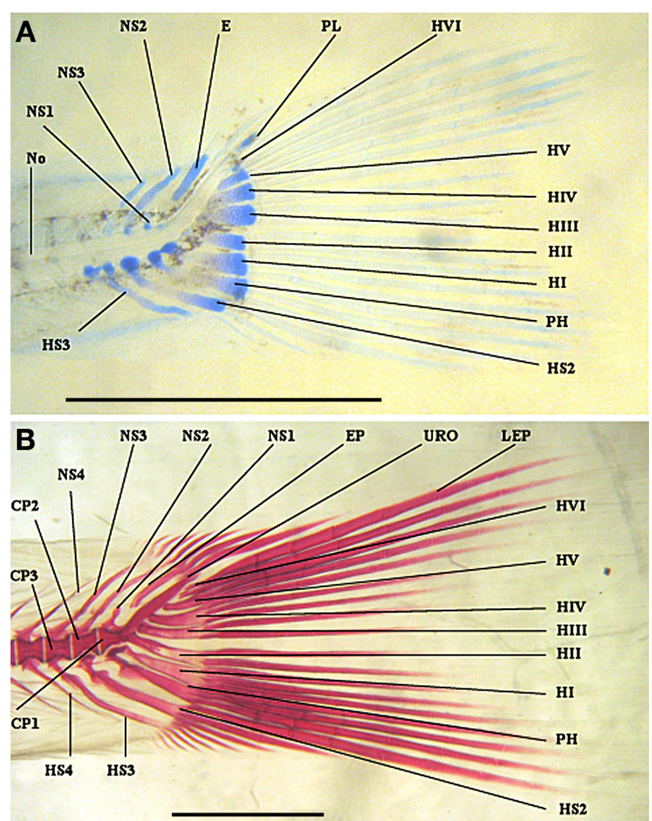

Figure 1. – *Labeo parvus* caudal fin structures. **A**: 14-day-old fry coloured with Alcian blue; **B**: 19-day-old fry coloured with Alizarin Red S. CP = preural centrum; EP = epural; H = hypural; HS = haemal spine; LEP = lepidotrichia; NO = notochord; NS = neural spine; PH = parhypural; URO = uroneural. Scale bars = 1 mm.

19 dph (Fig. 2E1)

The proximal parts of the axial caudal skeleton are not coloured with Alcian blue.

24 dph (Fig. 2F1)

Small components at the distal region of various elements remain cartilaginous.

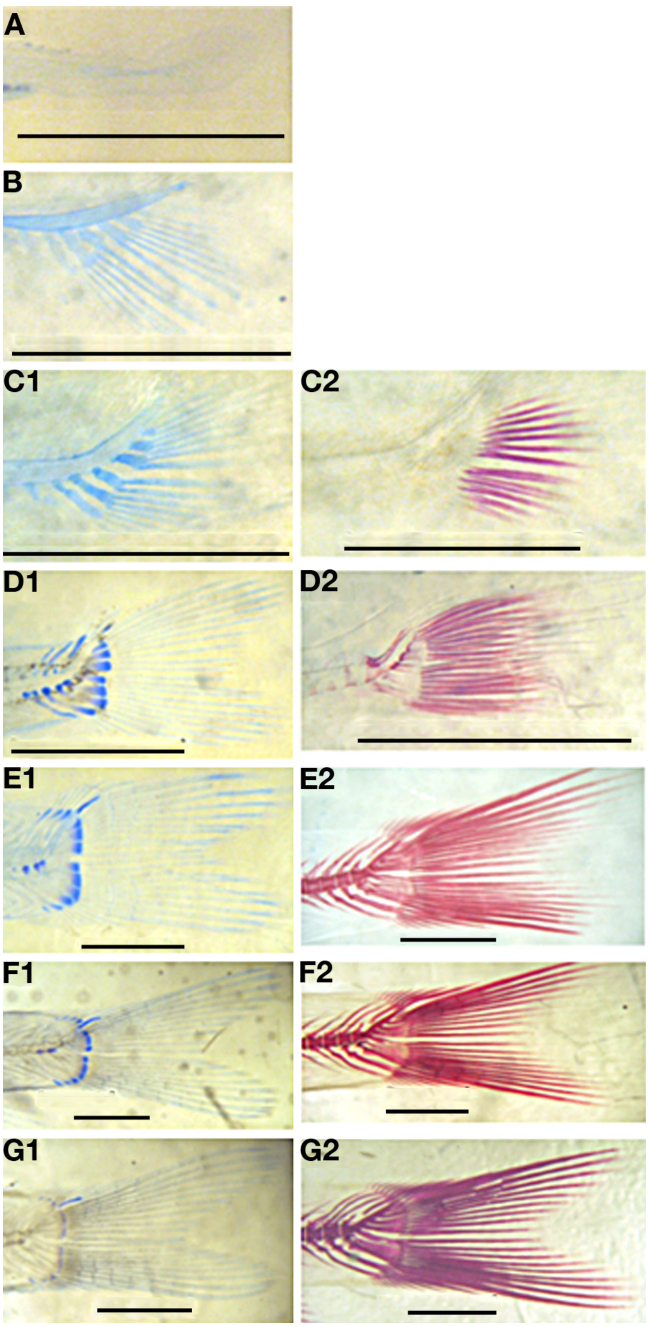

Figure 2. – Development of the caudal skeleton in *Labeo parvus*. Cartilaginous skeleton on the left column and osseous skeleton on the right column coloured with Alcian blue and Alizarin Red S, respectively. **A**: 6 days post-hatching (dph); **B**: 8 dph; **C**: 10 dph; **D**: 14 dph; **E**: 19 dph; **F**: 24 dph; **G**: 29 dph. Scale bars = 1 mm.

29 dph (Fig. 2G1)

Only the distal portion of the uroneural remains cartilaginous.

Osseous skeleton

10 dph (Fig. 2C2)

Twelve caudal rays are ossified.

14 dph (Fig. 2D2)

Ossification of the axial caudal skeleton begins. The first partially mineralized structures are the hypurals, the parhypural, the uroneural, and preural centra 1, 2, 3. Five additional caudal rays have ossified, bringing to 17 the total number of mineralized caudal rays.

19 dph (Fig. 2E2)

The caudal elements of the axial skeleton are ossified. Preural centra 1, 2 and 3, the parhypural, and hypurals are clearly visible. Haemal spines 2, 3 and 4, the epural, and neural spines 2, 3 and 4 have emerged. The first preural vertebra has an incomplete neural arch (NS1) and a long parhypural. Hypurals are most often fused to each other in their proximal regions and to the centrum of the first ural vertebra. However, some specimens display a hypural I, which is not fused to the centrum of the first ural vertebra. The parhypural is not always fused to the centrum of the first preural vertebra. In specimens where this is the case, the first hypural and the parhypural are fused in their distal parts. The first hypural expands towards the parhypural and they both eventually fused in their proximal parts. In all the coloured specimens, hypurals foramina can clearly be seen.

24 dph (Fig. 2F2)

The various elements retain their colour intensity.

29 dph (Fig. 2G2)

The developmental stage of the caudal elements is comparable to that of specimens observed on day 24; but they have mineralized further.

Dorsal fin development

Dorsal fin cartilaginous skeleton

Hatching to 10 dph

There is no trace of cartilaginous skeleton.

14 dph (Fig. 3A1)

Eleven pterygiophores are visible. Each consists of a distal pterygiophore and a proximal pterygiophore. Fin rays are visible attaching to distal pterygiophores. In all specimens, the first pterygiophore is related to the 8^{th} future vertebral segment. The 11 proximal pterygiophores cover 9 vertebrae.

The "concentration ratio" defined by François (1958) as the ratio of the number of fin endoskeletal parts (proximal pterygiophores) to the number of vertebrae in *L. parvus* is close to 1.2.

19 dph

The number of pterygiophores remains unchanged and these components (distal and proximal pterygiophores) are well developed. At this stage, the proximal pterygiophore already appears as a double cartilaginous structure. This is the beginning of the ossification process of this element, which usually starts in the middle region (François, 1958).

24 dph

The distal pterygiophores begin retreating and their development status is comparable to that observed in specimens of 14 days post-hatch. This retreat, which started at day 19 in proximal pterygiophores, still goes on along the entire length. The eleven proximal pterygiophores now are comparable to distal pterygiophores. Their middle region is not coloured with Alcian blue.

29 dph (Fig. 3B1)

The distal part of the proximal pterygiophore begins retreating and breaks into two cartilaginous islets. The first two distal pterygiophores are greatly reduced.

Dorsal fin osseous skeleton

14 dph (Fig. 3A2)

The first ossified elements appear; in most cases, the first seven dorsal lepidotrichia, but only the first six lepidotrichia are ossified in some specimens.

19 dph

The first seven pterygiophores are partially ossified, and the number of ossified lepidotrichia increase from 7 to 14. The first pterygiophore supports two lepidotrichia (2^{nd} and 3^{rd} lepidotrichia), as well as the 11^{th} pterygiophore (13^{th} and 14^{th} lepidotrichia). The other pterygiophores support only one lepidotrichia each. The first lepidotrichia, the shortest in the series, is directly connected to the first proximal pterygiophore.

24 dph

The lepidotrichia continue to develop.

29 dph (Fig. 3B2)

The first seven pterygiophores are now well ossified, while the 8^{th} and 9^{th} are ossifying.

Anal fin development

The development of the cartilaginous and osseous skeletons of the anal fin is fairly comparable to that of the dorsal fin. It provides the same organisational structure as the dorsal fin being only a little shorter.

Cartilaginous skeleton

14 dph (Fig. 3C1)

Six pterygiophores have appeared. They are each composed of a proximal and a distal pterygiophore as in the dorsal fin.

19 dph

The proximal pterygiophores starts retreating and takes the shape of a double cartilaginous structure: this is the beginning of the ossification. The number of pterygiophores remains constant.

24 dph

Both structures have significantly retreated. The proximal segment of the proximal pterygiophore shows only a few traces of Alcian blue. The distal pterygiophore is now reduced to a cartilaginous piece, which is quite comparable to that in a fry at 14 dph.

29 dph (Fig. 3D1)

The base of the proximal pterygiophore shows several translucent zones. The distal part of this structure is no longer cartilaginous. The distal pterygiophore remains cartilaginous; however, the intensity of staining has significantly decreased.

Osseous skeleton

14 dph (Fig. 3C2)

Three lepidotrichia have partially ossified.

19 dph

Seven lepidotrichia are ossified and the first four pterygiophores are partially ossified.

24 dph

The number of ossified lepidotrichia increases from 7 to 9. The development state of the pterygiophores is almost identical to that of specimens of 19 dph.

29 dph (Fig. 3D2)

This is the phase of strengthening: the four pterygiophores and the nine lepidotrichia have further mineralized.

Development of the vertebral column

Cartilaginous structures

Hatching to 10 dph

No structure is observed.

14 dph (Fig. 4A1)

The basiventrals are present under the first 13 or 14 vertebral bodies and under the last four. Each vertebra carries a pair of basiventrals except the 12th, the 13th, the 14th, the 33rd, the 34th and 35th. The basiventrals of the 4th and 5th vertebrae are more deeply coloured. The 3rd and 4th vertebrae and the last three (33rd, 34th, and 35th) carry the basidorsals.

19 dph (Fig. 4B1)

The basiventrals are visible under the first 17 and the last two vertebrae. The first 16 vertebrae carry each a pair of basiventrals. Those of the 4th to the 8th vertebra are more deeply coloured. The basiventral is not visible on the other vertebrae. The last three basidorsals are no longer stainable with Alcian blue as they have already reached an advanced stage of ossification. However, those of the 3rd and 4th vertebrae still are cartilaginous.

24 dph (Fig. 4C1)

A few bluish early basiventrals can be seen on the last two vertebrae. The other vertebrae carry neither basiventrals nor basidorsals, which results from gradual ossification of the haemal and neural arches.

29 dph (Fig. 4D1)

Cartilaginous structure can no longer be seen on the completely ossified haemal and neural arches of the vertebrae.

Osseous structures

10 dph (Fig. 4E)

The first ossification appears on the first three to four vertebrae. However, this is far from being a general rule since out of the five coloured specimens, only two have their first three or four vertebrae ossified.

14 dph (Fig. 4A2)

The 35 vertebral bodies are partially ossified but the degree of ossification varies widely: the first four vertebrae are ossified; from the 4th to 27th vertebrae, ossification is more or less homogeneous but these vertebrae are less coloured than the first four; the last seven are at an early stage of ossification and retain less Alizarin than the previous ones.

The first 14 basidorsals, except the first one, have already ossified. Some specimens show a seeming basidorsal on the last 10 or 12 vertebrae. In extreme cases, basidorsals already exist on all the vertebral bodies but are less ossified on their rear parts. Basiventrals 21 to 30 as well as those of vertebrae three and four have ossified. Some specimens display a seeming basiventral on the 5th vertebra.

19 dph (Fig. 4B2)

The vertebral bodies have mineralized further, and the haemal and neural arches as well as the ribs are ossified.

24 dph (Fig. 4C2) and 29 dph (Fig. 4C2)

The development stage is quite comparable to that of 19 dph specimens.

DISCUSSION

Caudal fin

The axial caudal skeleton supports lepidotrichia. However, it does not only provide support; it also ensures their mobility. The axial caudal skeleton largely acts as a fulcrum for the musculature and is situated in a region that plays an important role in fish propulsion. Some parts of this skeleton can play other roles, such as protecting the notochord, housing the caudal lymphatic hearts (by ensuring their connections through the central bone mass), ensuring blood flow to the edges of the body from the point where the haemal canal would have disappeared (Monod, 1968).

In *L. parvus*, the first elements of the cartilaginous axial caudal skeleton, hypurals I and II, appear on day 6 before notochord bending. At 44 to 48 hours post-hatching, *Cyprinus carpio* larvae already show many haemal elements (Rasoamananjara, 2004). By the time the notochord is bending, the five hypurals, the parhypural and a seeming haemal spine 2 have formed. In *C. carpio*, bending of the notochord occurs at approximately the same time as the first dorsal axial caudal skeleton such as the epurals and preural arches 1, 2 and 3 (Rasoamananjara, 2004). This dorsal, axial caudal skeleton is visible in *L. parvus* only on day 14, *i.e.* four days after notochord bending. In this species, the stage development of the cartilaginous axial caudal skeleton complex on day 14 is identical to that of *C. carpio* at 6 or 7 dph (Rasoamananjara, 2004). After a period of growth, the cartilaginous axial caudal skeleton starts retreating. This is a normal phenomenon encountered in all teleosts (Vandewalle *et al.*, 2005; Lederoun *et al.*, 2012). In this period, the osseous skeleton takes shape and gradually replaces the cartilaginous structures. In *L. parvus*, this begins on day 19; in *C. carpio*, it starts on day 8.5 (Rasoamananjara, 2004).

With regard to the mineralization of the tail fin, the rays ossify first, next the ventral elements of the caudal complex, then the dorsal structures. This ossification sequence is a general rule in teleosts (François, 1958).

Dorsal and anal fins

The dorsal, cartilaginous endoskeletal fin complex (pterygiophores) of *L. parvus* takes shape on day 14. As in most teleosts, it is made up of proximal and distal pterygiophores, the number of which varies among species. *L. parvus* possesses 11 pterygiophores, while *Salmo irideus* and *S. fario* have 12 or 13 pterygiophores (François, 1958). From a calcification perspective, the rays of the dorsal fin, ossify first in *L. parvus*, then anterior pterygiophores, and finally

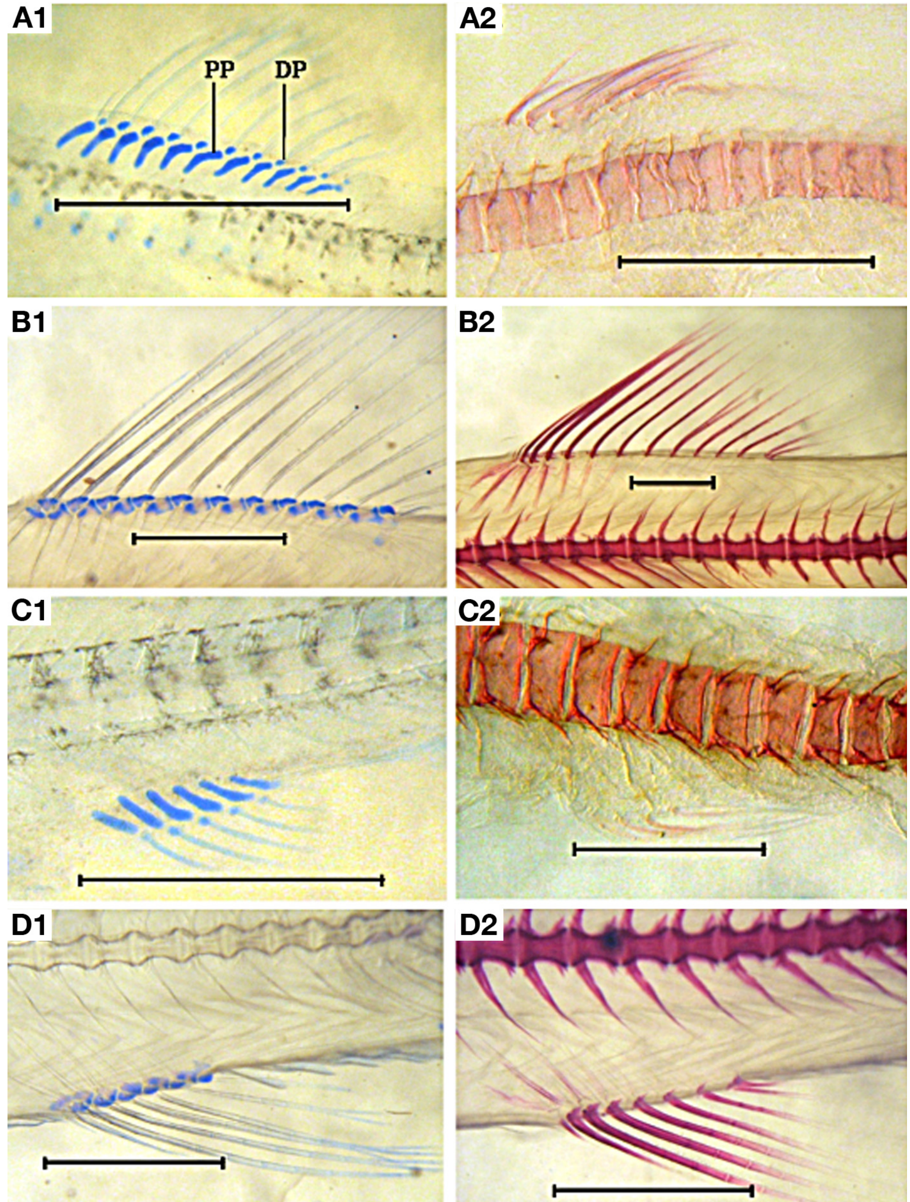

Figure 3. – Development of the dorsal and anal fin skeleton of *Labeo parvus*. Cartilaginous skeleton on the left, osseous skeleton on the right coloured with Alcian blue and Alizarin Red S, respectively. **A**, **C**: 14 days post-hatching (dph); **B**, **D**: 29 dph. DP: distal pterygiophore; PP: proximal pterygiophore. Scale bars = 1 mm.

the posterior pterygiophores. However, there seems to be a slight delay in the appearance of posterior pterygiophores in some specimens.

As observed in trout, distal pterygiophore seem to retain a cartilaginous structure for a long time. They can still be strongly coloured with Alcian blue in 29-day-old fry, in which they are superficially ossified as shown with Alizarin staining. Their ossification begins on day 30 in trout (François, 1958). The development of the anal fin is quite comparable to that of the dorsal fin. The anal fin has six pterygiophores, which each consists of a proximal and distal pterygiophores. As in the dorsal fin, the rays mineralize first, then the anterior pterygiophores, and finally the posterior pterygiophores. It should also be noted that a slight delay occurs in the appearance of posterior pterygiophores.

Vertebral column

The development of the vertebral column varies in teleosts (Potthoff and Kelly, 1982; Potthoff *et al*., 1986; Mabee, 1993; Potthoff and Tellock, 1993; Bui, 2003; Rasoamananjara, 2004). The first seeming cartilaginous structures begin taking shape in *L. parvus* on day 14 and appear in the most anterior and most posterior arches. In *C. carpio*, seeming basidorsal cartilaginous structures are visible on day 2.7 on the 3rd and 4th vertebra (Rasoamananjara, 2004). In *C. gariepinus* aged 2 days, seeming basidorsal cartilaginous structures are visible on the 3rd vertebra (Bui, 2003). In the anterior region of *L. parvus*, the basiventrals appear most often

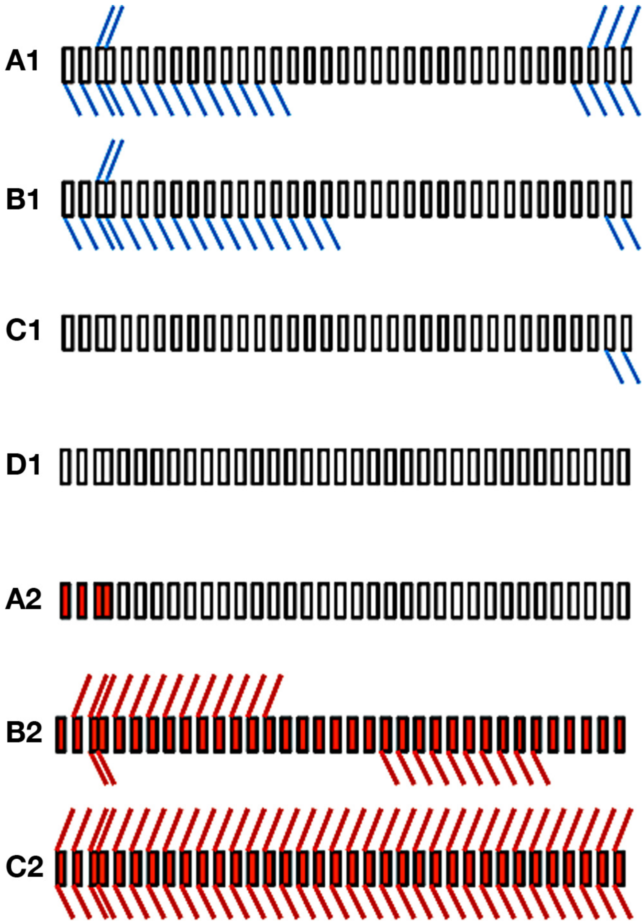

Figure 4. - Schematic representations of the development of the vertebral column in *Labeo parvus*. In blue: cartilaginous structures (neural basal dorsal and haemal basal ventral arches) as observed with Alcian blue staining. In red: development of the osseous structures (neural basal dorsal arch, haemal basal ventral arch, and vertebral structure) as observed with Alizarin Red S. **A**: 14 days post-hatching (dph); **B**: 19 dph; **C**: 24 dph; **D**: 29 dph.

in doubles: this is a general rule among cyprinids. This situation is also encountered in clupeids and salmonids (François, 1958). Only basiventrals of the 17 first vertebrae and those of the last three reveal seeming cartilaginous structures in *L. parvus*. In *C. carpio*, seeming cartilaginous basiventral structures are visible on all vertebrae with the exception of the first four (Rasoamananjara, 2004). Cartilaginous basidorsals are visible only on the 3rd and 4th vertebrae as well as on the last three. *Cyprinus carpio* shows seeming basidorsal cartilaginous structures on all vertebrae except the 2nd one (Rasoamananjara, 2004).

According to Bui (2003), during development *C. gariepinus* shows basidorsal cartilaginous structures on all vertebrae. In *L. parvus*, several vertebral haemal and neural arches are formed right away through ossification of the membrane. This is not a particularity of *L. parvus*. Indeed, François (1966) has described cases where, at certain spots on the vertebral column, or even on the entire vertebral column, appears no basal cartilaginous structure at any time. In *L. parvus*, the growth of endochondral bone in the arches seeming cartilaginous structures is much more precocious and faster. Even on the time of their appearance on day 14, mineralized parts are revealed by Alizarin staining. Arches go through the cartilaginous stage, which ossify first, meaning that ossification begins both in the anterior and in the posterior regions. In *C. carpio,* ossification of the arches begins in the anterior region (Rasoamananjara, 2004).

Ossification of the vertebral column starts with that of the anterior bodies as observed in *C. carpio* (Rasoamananjara, 2004). The particularity in *L. parvus* is the speed at which the vertebrae ossify. Within four days, the 35 vertebrae are ossified. The first vertebra is reduced to its vertebral body and the second is well-separated from the first. However, the third and the fourth are fused together. Those four vertebrae are part of the Weberian apparatus (Vandewalle, 1974). In *D. rerio*, Weberian centra (vertebrae 1-4) remain unfused throughout development, but in many fishes, the second and third centra may usually develop as a fused centrum (Bird and Mabee, 2003).

CONCLUSION

This study is a contribution to the breeding of *L. parvus*. We have investigated the development of axial and appendicular skeletons from hatching until 29 dph. The development of the vertebral column and unpaired fins occurs later than the cephalic skeleton. However, once started developmental processes are spectacular since all cartilaginous structures are formed within four days and the majority is then replaced by osseous structures. This allows larvae to improve swimming, the notochord to be protected, and the blood to flow to the edges of the fish body. In *L. parvus*, the formation of cartilage and bone in various parts of the skeleton follows the generally-observed process in teleosts, whereby various structures appear a little before or at the time they are adapted to play a role for species survival. From that point on, any changes of the formed elements or any delay in the development of the elements can be considered abnormal. This is therefore a reference point, which will guide future work on *L. parvus* farming in order to improve breeding conditions that are the key in the development of these skeletal elements in teleosts.

Acknowledgments. – The authors thank Emile N'tcha, Laboratory of Hydrobiology and Aquaculture of the University of Abomey-Calavi, Benin, for his help in the sampling of specimens; Frédérich Bruno and Eric Parmentier, Laboratory of Evolutionary and Functional Morphology, University of Liège, for the photographs and the valuable information they have provided along the way. The authors also thank the anonymous reviewers for their constructive comments.

REFERENCES

ARRATIA G., 1991. - The caudal skeleton of Jurassic teleosts; a phylogenetic analysis. *In*: Early Vertebrates and Related Problems in Evolutionary Biology (Chang M.M., Liu Y.H. & Zhang G.R., eds), pp. 249-340. Science Press, Beijing.

ARRATIA G. & SCHULTZE H.P., 1992. - Reevaluation of the caudal skeleton of certain actinopterygian fishes: III. Salmonidae. Homologization of caudal skeletal structures. *J. Morphol*., 214: 187-249.

BIRD N.C. & MABEE P.M., 2003. - Developmental morphology of the axial skeleton of the zebrafish, *Danio rerio* (Ostariophysi: Cyprinidae). *Dev. Dyn*., 228: 337-357.

BUI Q.T., 2003. - Impact du jeûne sur le développement du crâne et du squelette axial chez *Clarias gariepinus* (Teleostei, Clariidae). Travail de fin d'études, DES en Aquaculture. Univ. de Liège, Univ. Notre-Dame de la Paix de Namur, Belgique.

FAO, 2008. - Vue générale du secteur des pêches nationales: la République du Bénin. Profil des pêches et de l'aquaculture par pays. 4 p. FID/CP/BEN.

FRANÇOIS Y., 1958. - Recherche sur l'anatomie et le développement de la nageoire dorsale des téléostéens. *Arch. Zool. Exp. Gén*., 97: 1-108.

FRANÇOIS Y., 1966. - Structure et développement de la vertèbre de *Salmo* et des téléostéens. *Arch. Zool. Exp. Gén*., 107: 287-328.

FRASER M.R., ANDERSON T.A. & DE NYS R., 2004. - Ontogenic development of the spine and spinal deformities in larval barramundi (*Lates calcarifer*) culture. *Aquaculture*, 242: 697-711.

GRÜNBAUM T., CLOUTIER R. & DUMONT P., 2003. - Congruence between chondrification and ossification sequences during caudal skeleton development: a Moxostomatini case study. *In*: The Big Fish Bang: Proceedings of the 26th Annual Larval Fish Conference (Browman H. & Skiftesvik A.B., eds), pp. 161-176. Institute of Marine Research, Bergen.

KACEM A., MEUNIER F.J., AUBIN J. & HAFFRAY P., 2004. - Caractérisation histo-morphologique des malformations du squelette vertébral chez la truite arc-en-ciel (*Oncorhynchus mykiss*) après différents traitements de triploïdisation. *Cybium*, 28: 15-23.

LEDEROUN D., MONTCHOWUI E., LALÈYÈ P., PONCIN P. & VANDEWALLE P., 2012. - Développement postembryonnaire du squelette céphalique en relation avec les changements morphologiques externes chez *Labeo parvus* (Ostariophysi, poisson Cyprinidae). *Cybium*, 36: 383-396.

LÉVÊQUE C., 2003. - Cyprinidae. *In:* Faune des Poissons d'Eaux douces et saumâtres de l'Afrique de l'Ouest, Vol. 1 (Paugy D., Lévêque C. & Teugels G.G. eds), pp. 322-436. Collection Faune et Flore Tropicales n° 40. Tervuren: Musée Royal de l'Afrique Centrale; Paris (France): Muséum national d'Histoire naturelle & Institut de Recherche pour le Développement.

MABEE P.M., 1993. - Phylogenetic interpretation of ontogenic change: Sorting out the actual and artefactual in an empirical case study of centrarchid fishes. *Zool. J. Linn. Soc*., 107: 173-291.

MONOD T., 1968. - Le complexe urophore des poissons téléostéens. *Mém. Inst. Fond. Afr. Noire*, 81: 1-705.

MONTCHOWUI E., 2009. - Étude de la biologie de reproduction et de la multiplication artificielle d'une espèce de poisson Cyprinidae du bassin d'un fleuve Ouémé: *Labeo parvus* Boulenger, 1902, Bénin. Thèse de doctorat, 151 p. Univ. de Liège, Belgique.

MONTCHOWUI E., LALÈYÈ P., PHILIPPART J.C. & PONCIN P., 2007. - Biologie de la reproduction de *Labeo parvus* Boulenger, 1902 (Cypriniformes : Cyprinidae) dans le bassin du fleuve Ouémé au Bénin (Afrique de l'Ouest). *Cah. Ethol*., 22: 61-80.

MONTCHOWUI E., BONOU C.A., LALÈYÈ P., PHILIPPART J.C. & PONCIN P., 2011a. - Successful artificial reproduction of the African carp: *Labeo parvus* Boulenger, 1902 (Pisces: Cyprinidae). *Int. J. Fish Aquacult*., 3(3): 36-41.

MONTCHOWUI E., LALÈYÈ P., PHILIPPART J.C. & PONCIN P., 2011b. - Reproductive behaviour in captive African carp, *Labeo parvus* Boulenger, 1902 (Pisces: Cyprinidae). *J. Fish. Int*., 6: 6-12.

MONTCHOWUI E., AGADJIHOUEDE H., N'TCHA E. & LALÈYÈ P., 2012a. - Effets de milieux d'élevage sur la survie et la croissance des juvéniles de la carpe africaine, *Labeo parvus* Boulenger, 1902 en conditions contrôlées. *Int. J. Biol. Chem. Sci*., 6: 2131-2138.

MONTCHOWUI E., COMPÈRE P., THIRY M., LALÈYÈ P., PHILIPPART J.C. & PONCIN P., 2012b. - Histological assessment of gonad maturation in *Labeo parvus* Boulenger, 1902 (Teleostei: Cyprinidae) in Benin. *Afr. J. Aquat. Sci*., 37(2): 155-163.

MONTCHOWUI E., LALÈYÈ P., N'TCHA E., PHILIPPART J.C. & PONCIN P., 2012c. - Larval rearing of African carp, *Labeo parvus* Boulenger, 1902 (Pisces: Cyprinidae), using live food and artificial diet under controlled conditions. *Aquacult. Res*., 43: 1243-1250.

OSSE J.W.N. & VAN DEN BOOGAART J.G.M., 1995. - Fish larvae, development, allometric growth, and the aquatic environment. *ICES Mar. Sci. Symp*., 210: 21-34.

PATTERSON C., 1968. - The caudal skeleton in Lower Liassic pholidophorid fishes. *Bull. Br. Mus. (Nat. Hist.) Geol*., 16: 201-296.

POTTHOFF T. & KELLEY S., 1982. - Development of the vertebral column, fins and fin supports, branchiostegal rays, and squamation in the swordfish, *Xiphias gadius*. *Fish. Bull*., 80: 161-186.

POTTHOFF T. & TELLOCK J.A., 1993. - Osteological development of the snook, *Centropomus undecimalis* (Teleostei, Centropomidae). *Bull. Mar. Sci*., 52(2): 669-716.

POTTHOFF T., KELLEY S. & JAVECH J., 1986. - Cartilage and bone development in scombroid fishes. *Fish. Bull*., 84: 647-678.

RASOAMANANJARA H., 2004. - Impact du jeûne sur le développement du crâne et du squelette axial chez *Cyprinus carpio* (Teleostei, Cyprinidae). Travail de fin d'études, DES en Aquaculture. Univ. de Liège, Univ. Notre-Dame de la Paix de Namur, Belgique.

TAYLOR W.R. & VAN DYKE G.C., 1985. - Revised procedures for staining and clearing small fishes and other vertebrates for bone and cartilage study. *Cybium*, 9(2): 107-121.

VANDEWALLE P., 1974. - Contribution à l'étude anatomique et fonctionnelle de la région céphalique de *Gobio gobio* (L.) (Pisces, Cyprinidae). *Forma Functio*, 7: 47-54.

VANDEWALLE P., GLUCKMANN I. & WAGEMANS F., 1998. - A critical assessment of the Alcian blue/Alizarin double staining in fish larvae and fry. *Belg. J. Zool*., 128: 93-95.

VANDEWALLE P., GERMEAU G., BESANCENET P., PARMENTIER E. & BARAS E., 2005. - Early development of head skeleton in *Brycon moorei* (Pisces, Ostariophysi, Characidae). *J. Fish Biol*., 66: 996-1024.

VERHAEGEN Y., ADRIAENS D., DE WOLF T., DHERT P. & SORGELOOS P., 2007. - Deformities in larval gilthead sea bream (*Sparus aurata*): a qualitative and quantitative analysis using geometric morphometrics. *Aquaculture*, 268: 156-168.